THE MOLLUSCAN PERIOSTRACUM: AN IMPORTANT CONSTRAINT IN BIVALVE EVOLUTION

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ABSTRACT. The temporary, and often inconspicuous, nature of the bivalve periostracum has led to its relative neglect. As the first part of the valve to be secreted, onto which the calcareous shell is then deposited, the periostracum has great potential in governing basic valve form. Herein, periostracal thickness is shown to be an extremely variable character amongst members of the Bivalvia but within specific clades and life habits the range of variation is much narrower. It is suggested that differences in periostracal thickness have played a vital rôle in the evolution of different bivalve clades acting as an important preadaptation and constraint in the formation of various valve morphologies. Fine flexible periostraca allow the manufacture of intricate shell morphology and ornamentation, whilst a thickened sheet protects the calcareous part of the shell against environmental and biotic agents of dissolution.

Despite the poor preservation potential of the molluscan periostracum, its evolution and its primitive state are worthy of consideration. The distribution of periostracal thickness in Recent bivalves and the relative lack of fine ornament in early members of the class suggest that it was of at least moderate thickness. The findings of this survey have potential relevance to other molluscan classes and other phyla which use an analogous method of shell construction.

COMPARED with the attention that has been given to the microstructure of the calcareous part of the bivalve shell (e.g. Taylor *et al.* 1969, 1973; Carter 1990), little study has been made of its outer organic layer. The periostracum is the layer of sclerotinized protein which covers the exterior of the calcified shell of all shell-bearing molluscs, with the exception of members of the Polyplacophora. It is, however, easily removed by decay processes and hence its presence may often be overlooked. Within the class Bivalvia this organic sheet is of very variable character. It may be very obvious, as in the brilliant green outer covering of *Perna viridis*, or the shaggy outer layer of many arcoids, whilst in other taxa, for example ostreoids and pectinoids, it is scarcely detectable beyond the extreme valve edge. The occurrence of this organic layer as a discrete conchological entity was first recognized by Gray (1825) who named it the periostracum. Although he believed this structure to be wholly organic, more recent studies have shown that the periostraca of certain members of the Mytiloidea, Modiomorphoidea, Myoidea and Pholadomyoidea also contain calcareous elements embedded within the protein (Carter and Aller 1975; Bottjer and Carter 1980).

This paper considers some of the variation seen in the periostraca of Recent bivalved molluscs in particular in relation to their taxonomic position and their life habits, and considers its importance in the evolution of the class.

PERIOSTRACUM FORMATION AND FUNCTION

The periostracum is the first part of the shell to be formed. In the embryo, periostracum is secreted by the cells that border the shell gland (Kniprath 1979), whilst later in ontogeny this task is taken over by mantle tissue. With the increasing interest in the mechanisms of biomineralization (Carter 1990), periostracum formation has been studied in various gastropod and bivalve taxa, the findings of which have been reviewed excellently by Saleuddin (1980), Saleuddin and Petit (1983) and Watabe (1984). The process is briefly summarized here.

As with the rest of the shell, the periostracum is secreted by the mantle folds (Text-fig. 1).

Outer periostracum
- subject to decay and abrasion
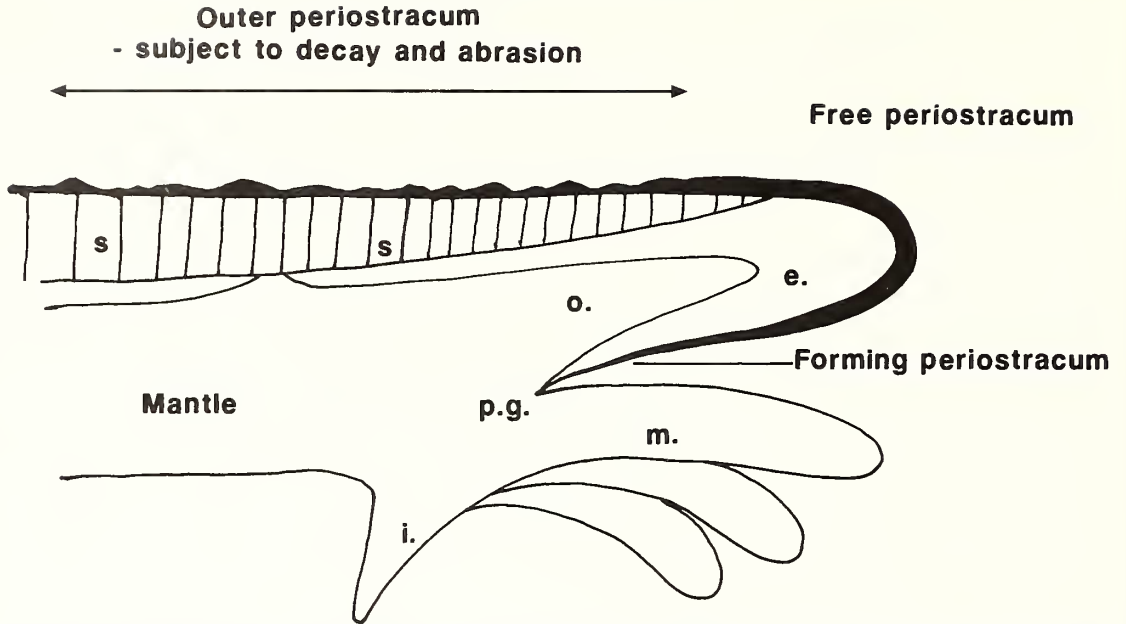
Free periostracum

TEXT-FIG. 1. Simplified valve and mantle margins of a generalized bivalve illustrating periostracum formation, following Saleuddin and Petit (1983). e. = extrapallial space; i. = inner mantle fold; m. = middle mantle fold; o. = outer mantle fold; p.g. = periostracal groove; s. = calcareous shell.

Saleuddin and Petit (1983) divided the periostracum into three zones; forming, free and outer periostracum. These terms are instructive when considering the development of the sheet and its function, although some of the terminology when referring to the inner and outer faces of the sheet is rather confusing. In the present account the inner face of periostracal sheet refers to the surface which is always closest to the cells of the outer mantle fold. The *forming periostracum* is initiated by cells at the base of the periostracal groove which lies between the outer and middle mantle folds. From here it moves ventrally as a continuous sheet between the two mantle folds, in close association with the middle fold. Epithelial cells of the middle fold along the route are responsible for further secretions thickening the sheet by addition of outer layers, and maturing it. Maturation involves sclerotinization by quinone tanning, a process which has been investigated for *Mytilus edulis* by Waite and Anderson (1980) and *Perna viridis* by Barranthi and Ramalingham (1989). The *free periostracum* spans from the edge of the mantle lobe to the extreme valve edge. Here it is freed from the influence of the mantle cells, being bathed on its inner surface by the extra-pallial fluid and on the outer surface by sea water. From this point no further thickening may occur. Just beyond the edge of the calcified shell the sheet doubles back upon itself, dorsally, so that it now covers the outside of the mantle lobe, becoming the *outer periostracum*. It is on to the inner surface of the reflected sheet that the calcareous shell is now seeded from the extra-pallial fluid. Exposed on the outside of the shell, the *outer periostracum* is subject to thickness diminution by physical and biotic abrasion and to fungal and bacterial decay.

The primary rôle of the periostracum is believed to be in shell secretion (Taylor and Kennedy 1969). Here it has two principal functions: first, as a template on which the calcareous part of the shell is initiated; Taylor and Kennedy (1969) have shown the intimacy between the periostracum and crystal growth by demonstrating the continuity of protein of the periostracum with that of the organic sheaths which surround the aragonite prisms of *Margaritifera margaritifera*; second, by providing a barrier between the extra-pallial space and the external aqueous environment, so allowing crystallization of either calcite or aragonite to occur in a compartment isolated from the

inhibiting presence of magnesium ions from sea water and from contamination by sediment (Clark 1976). In addition to these important rôles in shell secretion, a number of secondary functions have also been identified: protection of shell from the corrosive effects of acidic water (Tevesz and Carter 1980); protection from infestation by epibionts and endoliths (Bottjer 1981), and deterrence of predatory borers (Harper and Skelton 1993a). Araujo *et al.* (1994) showed the presence of extensions between the mantle and the periostracum in *Corbicula fluminea* and pointed out that these may allow the latter to play an active rôle in monitoring the environment also. These projections do not, however, penetrate the periostracal sheet.

Although there is a wealth of fine descriptive papers on the biology and functional morphology of a wide range of bivalves (see Morton 1992), few authors provide details of the periostracum. It is only in those taxa when it is conspicuously 'odd' (for example having a distinctive colour or ornament), and hence a useful character in species identification, that the periostracum is described. In most Recent taxa it seldom lasts intact throughout the life span of the mollusc, let alone surviving taphonomic processes. This poor preservation potential has led palaeontologists to pay even less attention to the periostracum than zoologists. There are very few published accounts of fossilized periostracum (discussed later). However, given the pivotal rôle that the periostracum plays in the construction and maintenance of bivalve (and most other molluscan) shells, particularly in the construction of ornament, it is likely to have also been influential in their evolution. Yet despite this importance there has so far been no attempt to discuss the taxonomic and adaptive significance of this variation.

PERIOSTRACAL THICKNESS IN THE BIVALVIA

Even a cursory foray through the literature on Bivalvia reveals that one of the periostracal characters which is most variable is thickness. It is, generally, those taxa with the greatest periostracal thickness that have the more persistent and hence more conspicuous periostraca, and the literature on bivalve periostraca is biased towards the description of these. Detailed accounts of its formation and structure have dwelt on taxa with substantial periostraca, for example *Mytilus edulis* (Dunachie 1963), *Anodonta cygnea* (Bubel 1976), and *Astarte castanea* and *A elliptica* (Saleuddin 1974). Such a bias is, at least partly, explained by the relative ease of manipulation and investigation of these more robust structures compared with the gossamer-thin sheets of other bivalves. In the literature, terms referring to thickness include 'thick', 'thin' and 'excessively thin'. Using such qualitative terms may be misleading for, often, taxa with darker periostraca give an erroneous impression of being thicker than those which are more translucent, and the lack of agreed conventions about these descriptions means that they are very subjective and of little use when comparing taxa. For example, Morton (1974) refers to the periostracum of *Cleidothaerus maorianus* as 'thin', yet it is at least an order of magnitude thicker than that of virtually all pteriomorphs and of many of the heteroconchs. Precise measurement, however, may be difficult, and the value obtained will vary depending on where it was taken, lower values being recorded in the forming periostracum where it is yet to attain its full thickness, or the outer periostracum where material has been lost. For comparative purposes it is essential that measurements are made from the free periostracum where thickness is neither increasing or decreasing, or from the outer periostracum in cases where it is judged to be intact. Although the periostracum produced by the very earliest juvenile individuals is less substantial than that of the full-grown adult, no evidence has been published of thickness variation in the dissoconch stage of any taxon.

Is periostracal thickness important? Are various clades characterized by periostracum of a particular range of thicknesses? A number of possible links between periostracal thickness and various life habits and surface ornamentation may be suggested: e.g. Harper (1992) suggested that an ultra-thin periostracal sheet is essential for the cementation process, whilst Taylor and Kennedy (1969) and Kennedy *et al.* (1969) pointed out that bivalves which use chemical secretions to bore into hard substrates are covered in thick, protective periostraca. Are such perceived links important preadaptations in the evolution of certain habits, selected by that particular habit (i.e. adaptive) or merely coincidental? In this context the term preadaptation is used as defined by Skelton (1985,

p. 95) as 'a feature or a complex of features of an organism, whether already serving a functional role or merely a constructional product, which by virtue of its *fortuitous* suitability for novel functional effects becomes *co-opted* as a new adaptation…in descendants of the organism'. There is no implication of consciousness.

Since the periostracum is the first formed part of the shell and subsequent shell layers are deposited onto it, it must form the template for the ornamentation of the outside of the valve. It is not possible to create the calcareous part of the shell in a particular shape unless this has already been described by the periostracum. Thus the intricacy and extravagance of the surface ornamentation must depend, at least in part, on the flexibility of the periostracal sheet. In this context, surface ornamentation is taken to mean the occurrence of ribs, spines, flanges, furrows and ridges and tubercles on the external surface of the calcareous shell. Two models for the production of valve ornament in bivalves (or indeed other molluscs) may be advanced: (1) the periostracum maintains a constant thickness and the ribbed ornament is achieved by folding the sheet; and (2) the periostracum is of variable thickness and the inner surface is sculpted to provide a negative of the ornament. Can studies of periostracal thickness be used to differentiate between these two models? In order further to investigate these questions, the taxonomic and adaptive significance of periostracal thickness within the Bivalvia is discussed in detail below.

MATERIALS AND METHODS

Collections of living bivalves were made during field work in the United Kingdom, Hong Kong, Panama and the eastern coast of Australia. Entire animals were fixed in either 3 per cent. glutaraldehyde, 70 per cent. ethanol or 5 per cent. neutral formaldehyde, depending upon availability. In order to sample as large a range of taxa as possible, covering a wide geographical area, material was also assembled from the 'wet' collections of The Natural History Museum (London) and the Australian Museum (Sydney), whilst Antarctic species were made available by S. Hain from the Alfred-Wegener Institute (Bremerhaven, Germany). In all cases only fully grown animals were used.

In the majority of cases fixed animals were opened and mantle tissue was excised from the ventral edges of the right mantle lobe. Although it has yet to be demonstrated conclusively that there are any significant differences between various characters of the right and left mantle lobes of any bivalve species, this consistency of approach was used to negate the effect of any such variation. It is not anticipated that the mantle lobes of equivalve taxa are any different, but the possibility cannot be discounted for those which have inequivalve or discordant morphologies. Once so obtained, the mantle tissue was dehydrated through a series of acetones and then critical point dried, using carbon dioxide as the ambient fluid, in the manner described by Martill and Harper (1990).

In taxa which possess a particularly thick periostracum the time-consuming process described above was avoided. In these instances individuals were inspected with a binocular microscope to select areas with no damage to the periostracum on the ventral shell margin (therefore no thickness loss) and these areas removed.

Once so prepared the specimens were mounted on stubs, sputter coated with gold and inspected using scanning electron microscopy (Jeol 820). Periostracum suitable for measurement was identified as it emerged between the mantle folds and the specimens were tilted so that the fractured edge of the periostracum was perpendicular to the electron beam so as to reveal true thickness. The fractured edges were photographed for later measurement; additional information, such as the presence of spicules, vacuoles, obvious layering and hairs, was also noted.

Additional thickness data were also obtained by recording existing measurements mentioned in the literature, or by measuring directly from previously published photographs. Caution was required in this approach because it is uncertain from which part of the periostracum these were taken. Only 7 per cent. of the data-base was acquired in this manner.

The possibility of intraspecific variation of periostracal thickness must be considered, particularly as the time involved in preparation and the scarcity of some of the material meant that it was

often impracticable to make measurements from more than one individual. Without carrying out an extensive survey it is impossible to rule out such a problem; however, earlier work (Harper 1992) on the mantle margins of several hundred individuals of the oysters *Crassostrea gigas* and *Ostrea edulis* revealed no significant variation in periostracal thickness. Comparison of measurements made in this study with figures published by other authors for the same taxa also revealed no significant differences. However, intraspecific variation does occur: periostraca of *Mytilus edulis* from different localities showed a variation of some 20 per cent. in sheet thickness (Harper 1991).

In order to examine the two models of ornament formation, individuals of bivalve taxa with strong radial ornament, such as the mytiloids *Septifer virgatus*, *Geukensia demissa* and *Hormomya mutabilis* and the veneroids *Donax panamensis* and *Prototharca megintyi* (which had intact periostracal cover) were selected. These valves were cut along lines normal to the radial ornament and then studied using SEM. Specimens of *Mya truncata*, an anomalodesmatan bivalve, were also examined. Although largely smooth, they commonly show wrinkling on the posterior part of the shell. The task of examining the relationship between periostracum and more intricate styles of ornamentation, such as spines and flanges, was rather more problematical, as there is no universally accepted measure of valve ornament. Although Stanley (1970) produced an ornamentation index for his study on burrowing efficiency, it is unsuitable for the present work because it deals with overall relief rather than expressing the radius of curvature, ornament depth, spacing or aspect. Instead Nicol's (1965) survey of spinose and non-spinose families was used as a basis of the analysis.

RESULTS AND ANALYSES

Periostracal thickness measurements were obtained for more than 450 bivalve species. The data are presented in Appendix 1. For analysis, each taxon was assigned to its family, and hence into one of the seven major groupings used by Skelton *et al.* (1990): protobranchs, arcoids, mytiloids, pteriomorphs, heteroconchs, lucinoids and anomalodesmatans, which they regarded as mono-phyletic clades. Each taxon was also assigned to one of five life habits: burrowing within a soft sediment (with some distinction between shallow and deep burrowers), byssate attachment, boring into hard substratum, attachment to a hard substratum by cementation and free-living on the sediment–water interface. Such designations were based on either personal observation at the time of collection, previously published accounts, or on functional morphological criteria (as in Stanley 1970). Stanley (1970) recognized a further two types of life habit: nestling and reclining. Most nestlers are also byssally attached and so these bivalves were placed in the latter category (see also Nicol 1983), and the recliners were grouped with the free-livers.

A very wide range of periostracal thickness was recorded from values of less than 1 μm in a number of taxa to 428 μm in the mussel *Musculus laevigatus*. Within this range nearly 60 per cent. of those taxa studied had periostraca less than 10 μm thick. Such a wide range with its strong negative skew makes linear plots difficult to handle and, therefore, it was decided to utilize a logarithmic scale. This led to the recognition of seven thickness classes (Table 1).

TABLE 1. Periostracal thickness classes and their descriptive terms.

| Thickness (μm)	Descriptive term used herein
< 1·0	Ultrathin
1·0–3·16	Thin
3·17–10·0	Moderate
10·1–31·6	Thick
31·7–100	Very thick
101–316	Grossly thickened
> 317	Grossly thickened
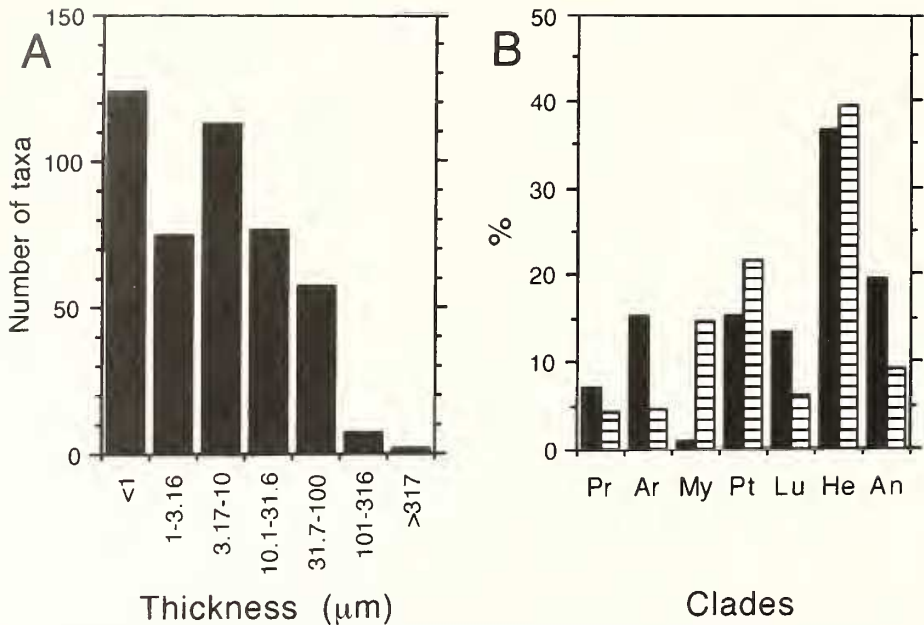
TEXT-FIG. 2. A, distribution of periostracal thickness for the entire data set. B, histogram demonstrating the bias of the data set; dashed bars show the percentage of extant bivalve families which fall into each clade and solid bars the percentage of taxa from this study belonging to each. An = anomalodesmatans; Ar = arcoids; He = heteroconchs; Lu = lucinoids; My = mytiloids; Pr = protobranchs and Pt = pteriomorphs.

Taxonomic variation

Text-figure 2A shows the distribution of periostracal thickness observed for the entire data set. Such a plot cannot be considered as representative of the variation in this parameter for the class Bivalvia, as it is undoubtedly biased by the specifics of the set, for example by the over-representation of pteriomorphs and mytiloids and the comparatively low number of anomalodesmatan, lucinoid and arcoid species measured (Text-fig. 2B). Only the lucinoids were seriously under-sampled; of the 13 extant families only seven were investigated. Such incomplete coverage was, in part, due to the small size and fragility of members of the missing families, and their paucity in museum collections. Both of these reasons are in turn the result of their mainly cryptobyssate habits (Yonge and Thompson 1976). Histograms showing the range of periostracal thickness recorded in each clade are given in Text-figure 3, and are discussed below, together with statistical analyses of their significance.

Protobranchs. Members of the protobranch clade are characterized by a moderate to thick, obvious and persistent periostracum (Text-fig. 3A). The thickness recorded for these taxa ranges between 3 μm for *Leda minuta* and *Nucula nucleus* to over 100 μm for species of *Solemya*. Measured *S. borealis* attain a periostracal thickness of 100 μm, whilst Beedham and Owen (1965) reported that of *S. parkinsoni* as being 140 μm. In the solemyoids the periostracum extends ventrally some way beyond the edge of the calcareous shell to form a flexible, radially pleated flange, which Beedham and Owen (1965) showed to be in intimate contact with the mantle epithelium, being the site of orbicular muscle insertions. In all protobranchs examined, the periostracum was smooth with no external ornament or indication of internal structures.

Arcoids. Arcoids appear to possess a very thick and persistent periostracum (Text-fig. 3B). However, in many genera, e.g. *Limopsis* and *Glycymeris*, the layer is densely covered by conspicuous hairs, the presence of which often makes the precise thickness of the sheet difficult to ascertain. In fact, when
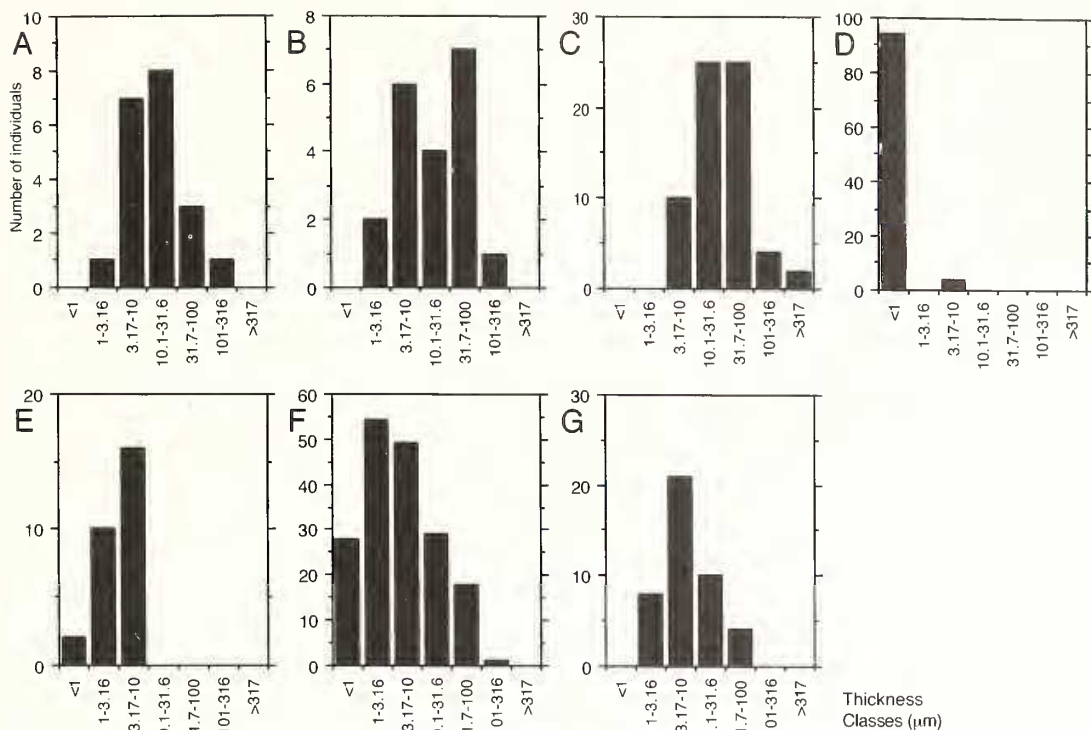
TEXT-FIG. 3. Histograms showing the range of periostracal thickness recorded for each clade. A, protobranchs; B, arcoids; C, mytiloids; D, pteriomorphs; E, lucinoids; F, heteroconchs; G, anomalodesmatans.

one subtracts the thickness of the hairy sub-layer, the basal sheet, to which the hairs are attached, is only moderately thick. For example, *Limopsis marionensis* has a very conspicuous shaggy pile attached to a sheet of a mere 5 μm thickness. Hair formation in arcoids has been described by Waller (1980) who argued that they are formed during maturation of the periostracal sheet, and not under direct mantle control.

Mytiloids. This clade comprises one extant family, the Mytilidae, but contains a great diversity of genera and species. In general the mussels possess a particularly thick and persistent periostracum, and have the thickest periostraca recorded herein (Text-fig. 3c). The recorded range is from 5 μm for *Ciboticola lunata* (a questionable mytilid; Moore 1969) to 428 μm for *Musculus laevigatus*. The median value for the data sub-set was 30 μm, with seven taxa registering values of over 100 μm.

The mytiloids also display a range of periostracal structures. As noted by Dunachie (1963) the periostracum of *Mytilus edulis* is tri-layered (Text-fig. 4A), the central layer often being vacuolated. This layer is not continuous over the entire periostracal area, and its adaptive significance is not clear. Such vacuolation has not been observed in the periostracum of other mussels studied. Hairs were encountered in a number of taxa, e.g. *Modiolus modiolus*, *Modiolus capax* and *Trichomya hirsutus*. They are not simple projections but display a variety of flattened, serrated and palmated morphologies as illustrated by Ockelmann (1983). The functional morphology of these structures was discussed by Bottjer and Carter (1980) who suggested a variety of functions, for example supplementation of shell ornamentation for stabilization, extension of mantle sensors and deterrence of settling by fouling epibionts. These authors considered that the hairs are produced by the outer middle mantle fold, but Ockelmann (1983) observed their formation in *Modiolus* and juvenile *Mytilus* on areas of the shell away from the valve edges (and hence away from mantle
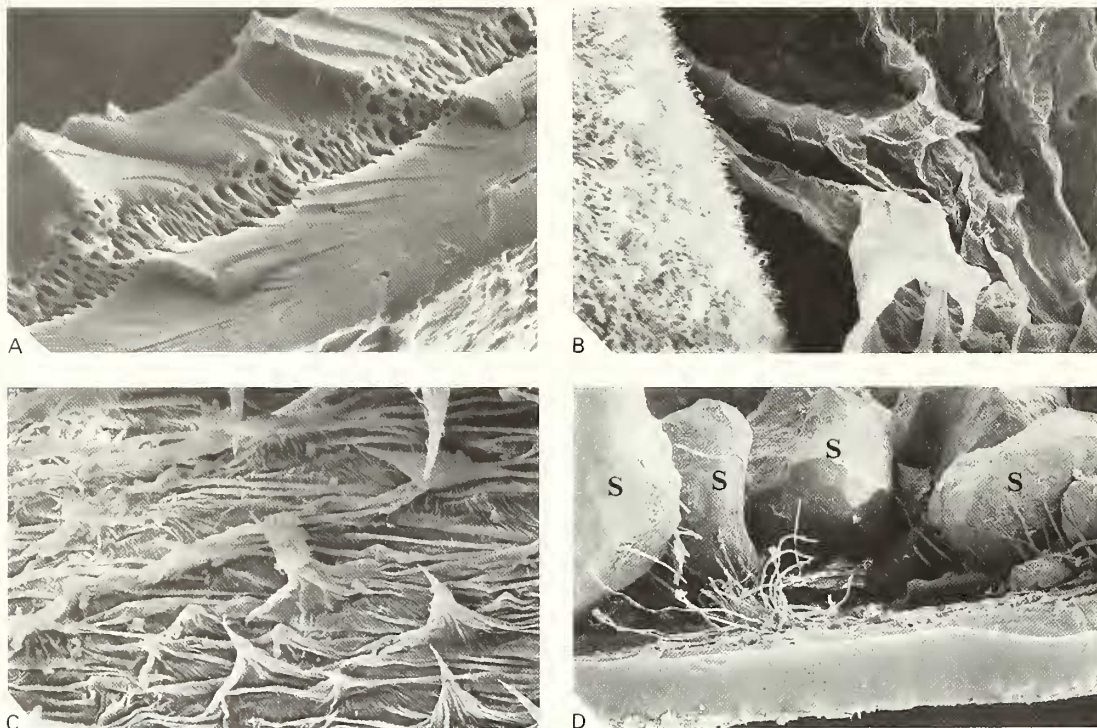
TEXT-FIG. 4. A, *Mytilus edulis* (mytiloid); SM X.27504; Oban, UK; note the vacuous middle layer; × 1500. B, *Pinna saccata* (pteriomorph); SM X.27505; New Caledonia; note the fine, wrinkled periostracal sheet emerging from beside the ciliated surface of the middle mantle fold; × 500. C, *Cardita affinus* (heteroconch); SM X.27506; awn-like processes arising on the outer surface of the fine periostracal sheet; × 500. D, *Lyonsia norwegica* (anomalodesmatan); SM X.27507; Northumberland, UK; note adherent sand grains (S) on outer surface of periostracum; × 1500.

influence). He concluded that they are, like the byssus, produced by the foot and further noted that taxa with the greatest development of these hairs are also those with large anterior byssal gland complexes.

Pteriomorphs. Extremely thin (< 1 μm) periostracal sheets characterize virtually all of the pteriomorph taxa measured (Text-figs 3D, 4B). Fourteen of the 15 extant families of this clade possess such a gossamer-thin sheet that is not easily perceived on the external surface of the shell, and indeed seldom persists past the valve margins. Only in the Anomiidae were thicker periostraca recorded, for example *Anomia ephippium* (10 μm), *A. archaeus* (8 μm) and *Monia squamosa* (10 μm).

Lucinoids. Members of this clade possess a moderately thick periostracum (Text-fig. 3E), the highest values recorded being 10 μm for *Diplodonta diplodonta* and *Myrtea botanica*. The periostracum is often conspicuous as a straw-yellow, varnish-like coating to the shell, and is reasonably persistent.

Heteroconchs. The heteroconch clade is the largest considered here, with 36 extant families, and displays the greatest variation in periostracal thickness (Text-fig. 3F). Values as thin as 1 μm (or less) have been recorded in 15 taxa, whilst the thickest periostracum measured was that of *Trapezium sublaevigatum* at 110 μm. Despite the large range for the clade, that within constituent superfamilies is much narrower, for example Arcticoidea 70–110 μm, Chamoidea 1–2 μm, most Cardioidea

1–2 μm and Solenoidea 10–50 μm. There is also great variation in periostracal structures and ornaments within this clade. Many taxa bear smooth, apparently featureless, periostracal sheets whilst others show a range of ornaments and structures. The external surface of the periostracum of members of *Astarte* shows a reticulate ornament (see Saleuddin 1974, figs 16–17), whilst several of the carditids (e.g. *Cardita affinis*, see Text-fig. 4c) have hairy periostraca.

Anomalodesmatans. These possess a moderate to thick, persistent periostracum (Text-fig. 3g). The finest measured was 2 μm for *Jouneltia cumingi*, whilst the thickest recorded belonged to *Lyonsia norwegica* at 80 μm. Members of the clade also display a number of interesting periostracal features, for example the development of calcareous elements within the organic periostracum (Carter and Aller 1975). Aller (1974) described how calcareous spicules, manufactured by the outer mantle fold of *Laternula flexuosa*, are incorporated into the periostracal sheet where they may provide stabilization. Carter (1978) described similar spicules in the periostracum of the boring gastrochaenid *Spengleria rostrata*, which he considered may aid the boring process. Other anomalodesmatans, including many of the Pandoroidea, appear to be characterized by having a 'sticky', semi-fluid outer layer to the periostracum. In the lyonsiids, sand grains and other debris adhere to this mucoid layer (Text-fig. 4d), which Prezant (1981) believed may camouflage and protect the shell, or assist with stabilization within a shifting substratum. He described the presence of arenophilic glands within the outer mantle fold which, in *Lyonsia*, he suggested secreted the mucoid into the periostracal groove on to which the rest of the periostracum is then secreted, whilst in *Entodesma* he suggested that the glands are positioned more distally and secretions pass through the periostracum, perhaps by localized dissolution of the sheet. However, Morton (1987a) has shown that such glands in members of the Thracioidea, Pholadomyoidea and Clavagelloidea are located in the middle mantle folds where they empty on to the (eventual) outside of the newly formed periostracum.

Analysis. The Mann–Whitney test was used to test for significant differences in location between pairs of clades to ascertain whether apparent differences were valid. The results of these tests are

TABLE 2. Results of the Mann–Whitney test for the significance in location between pairs of clades. In the upper right hand portion of the table significant differences at the 5 per cent. level are marked +, whilst non-significant differences are marked ×. The calculated percentage significances are given in the lower left part of the table.

	An	Ar	Het	Luc	Myt	Pr	Pter
An	—	+	+	+	+	+	+
Are	5%	—	+	+	×	×	+
Het	0·25%	0·05%	—	×	+	+	+
Luc	0·08%	0·01%	97·5%	—	+	+	+
Myt	0%	9·0%	0%	0%	—	×	+
Pr	1·4%	89·9%	0·01%	0%	7·9%	—	+
Pter	0%	0%	0%	0%	0%	0%	—

shown in Table 2. At the 5 per cent. level most were significant except the following pairs: heteroconch and lucinoid, arcoid and protobranch, arcoid and mytiloids and protobranch and mytiloids. Using a Wilcoxon test, 95 per cent. confidence intervals were established for the median of each clade (Table 3). These show clearly that the anomalodesmatan, heteroconch, pteriomorph and lucinoid clades display relatively small ranges of periostracal thickness, whilst in the others the range is far greater. It is also clear that although there is a great deal of similarity in the thicknesses shown by members of the arcoid, mytiloid and protobranch clades, the others are more distinct, albeit with some overlap.

TABLE 3. Results of the Wilcoxon test to establish the 95 per cent. confidence interval for the median value of each clade.

Clade	95 per cent. confidence intervals (μm)
Anomalodesmatans	7·5–12·5
Arcoids	10·0–52·5
Heteroconchs	2·2–8·5
Lucinoids	3·5–6·0
Mytiloids	26·5–45·0
Protobranchs	11·5–54·0
Pteriomorphs	0·5–0·5
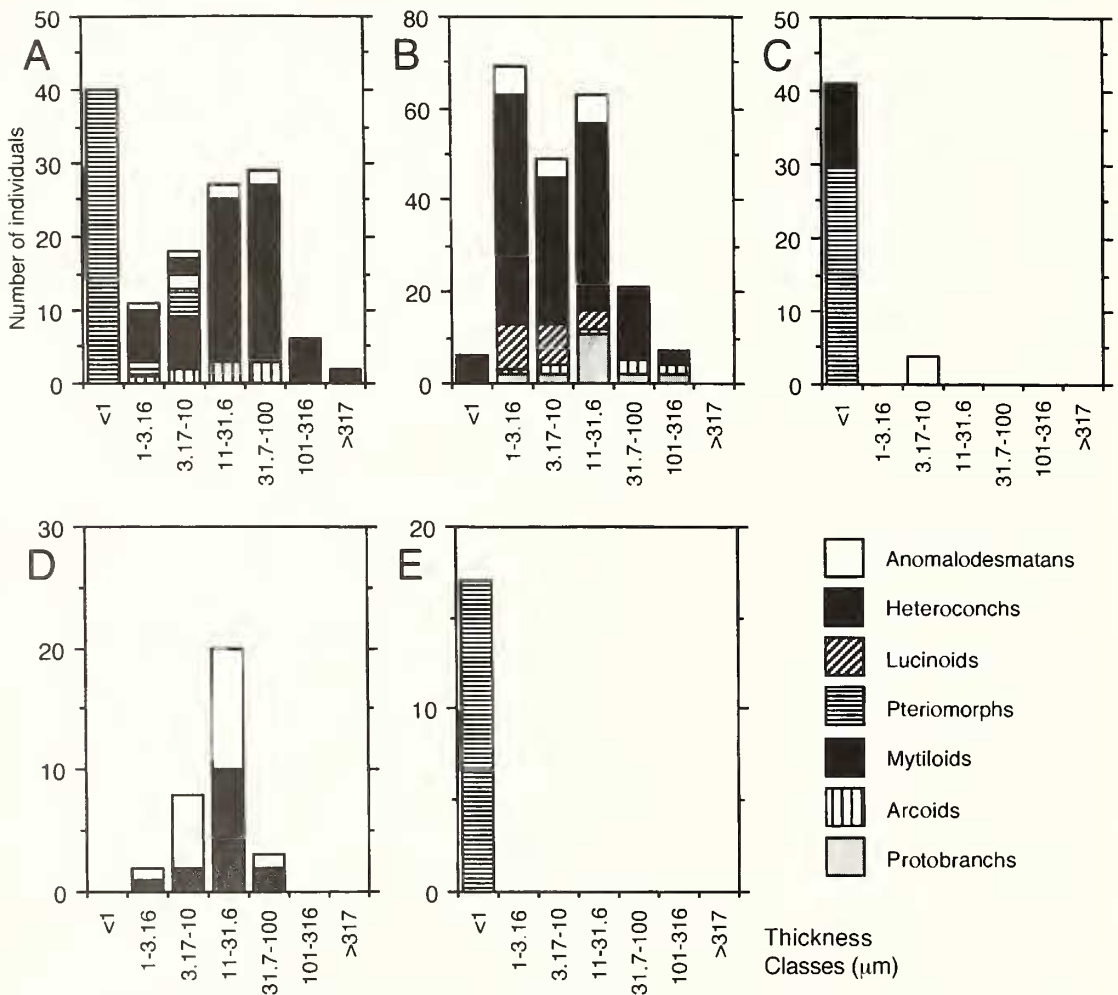
TEXT-FIG. 5. Histograms showing the periostracal thickness recorded for different life habits, A, byssally attached; B, burrowers; C, cementers; D, borers; E, free living (including nestlers and recliners).

Life habits

Text-figure 5 shows the distribution of periostracal thickness in the exponents of various life habits. The byssate and burrowing habits are exploited by a number of bivalves, not limited to those with a specific periostracal value. It is, however, worth noting that those taxa which have acquired convergently the ability to burrow to great depths, such as *Tagelus* (Tellinoidea), *Solemya* (Solemyoidea), and *Solen*, *Pharella* and *Ensis* (Solenoidea) are characterized by thick periostraca. A thick periostracum is shared by those which are active deep burrowers and those which live entombed at depth. Of the more specialized habits, cementers and free-living bivalves appear to be dominated largely by taxa possessing an ultra-thin periostracum, whilst the borers belong to clades with at least moderate development of the periostracal sheet. Possible adaptive significance of these findings are discussed below.

Analysis. As above, the Mann–Whitney test was used to test for the significance of differences in location between each pair of life habit groupings. These results are shown in Table 4. At the 5 per

TABLE 4. Results of the Mann–Whitney test for the significance in location between pairs of life habit groups. In the upper right hand portion of the table significant differences at the 5 per cent. level are marked +, whilst non-significant differences are marked ×. The calculated percentage significances are given in the lower left part of the table.

	Borer	Byssate	Cementer	Burrower
Borer	—	×	+	+
Byssate	16%	—	+	×
Cementer	0%	0%	—	+
Burrower	0·06%	21%	0%	—

cent. level there were significant differences for all pairs except two: borers and byssate, and byssate and burrowers. Table 5 shows the 95 per cent. confidence interval ranges of periostracal thickness for each life habit calculated by the Wilcoxon test. The wide range of values displayed by byssate taxa overlaps with those of the borers and burrowers, although the latter two can be distinguished. The narrow ranges shown by cementers and free-living taxa are well separated from the other life habit groups, but are not distinguishable from one another.

Relationship to ornament

Bivalve taxa with pronounced radial ornament, and the 'wrinkled' shells of *Mya truncata* show no evidence to support the second model of ornament formation. In all cases examined, the periostracal sheet maintained even thickness over the ridges and troughs. There are some instances where bivalves have a very fine scale of surface ornamentation which does appear to support Model 2, for example micro-tubercles (a few micrometres in diameter) on the surface of neotrigoniids (Taylor *et al.* 1969) and *Myochama* (pers. obs.) fit into corresponding depressions on the inner surface of their periostraca. However, as shown by Taylor *et al.* (1969), these depressions are actually caused by the growth of prismatic crystals and post-date the formation of the periostracal sheet.

  Nicol (1965) noted that the families which make up the clades here considered as protobranchs, arcoids, mytiloids, anomalodesmatans and most of the lucinoids never bear spines. As noted above these are clades with at least moderately thick periostraca. By contrast, the pteriomorphs, with their mostly ultra-thin periostraca, contain some of the most extravagantly ornamented families (e.g. Spondylidae, Ostreidae and Pectinidae). The heteroconch clade contains both virtually unorna-

Life habits	95 per cent. confidence intervals
Borers	11·5–19·5
Byssate	10–25
Cementer	0·5–0·5
Burrower	6·5–10
Free living	0·5–0·5

TABLE 5. Results of the Wilcoxon test to establish the 95 per cent. confidence interval for the median value of each life habit group.

mented (e.g. solenoids, most venerids and mactrids) and very spiny families (chamids, cardiids and some venerids (e.g. *Pitar* and *Chione*)).

INTERPRETATIONS

In this survey it has been shown that although there is a great variation of periostracal thickness within the Bivalvia, specific clades, life habit groups and styles of ornamentation are characterized by much narrower ranges. Is there any evolutionary significance to these observations?

In his review of Ordovician bivalves Pojeta (1978) considered them to be predominantly either shallow non-siphonate burrowers or forms that were byssally attached either within (endobyssate) or on (epibyssate) the sediment. Both of these life habits may be considered as primitive within the Bivalvia, from which all the other life habits were ultimately derived. Several authors have suggested that many of the specialized life habits have a defensive value and appear to have evolved chiefly after, and in direct response to, the increase in predation pressure at the beginning of the Mesozoic (Vermeij 1987; Harper and Skelton 1993b). They observed that one of the most interesting aspects of the adaptive radiations of the bivalves is identifying the constraints and preadaptations which have determined the pathways taken by various clades. Is it possible that the form, in particular the thickness, of the periostracum may have had an important influence?

Shallow burrowing and byssate bivalves show a wide range of periostracal thickness and it is difficult to argue that there is any particular primary advantage to any of these, although there are secondary advantages, as discussed above. Patterns only develop when considering the more specialized life habits, and where the acquisition of new habits has been polyphyletic it may be possible to test whether certain habits are associated with particular periostracal characters.

Particularly thin periostracal sheets appear to correlate with the cementing and free-living modes of life. The cementing bivalves examined include members of each of the nine clades of extant marine forms of these (Harper 1991). All but two of these clades are characterized by the possession of an ultra-thin periostracum. Harper (1992) considered that the ability of these cementers to construct their shells in extremely close proximity to the micro-topography of the substratum is vital to their attachment. This by necessity means that they have a very thin periostracum, and Harper (1991, p. 45) noted that 'no periostracum can follow substratal irregularities whose radii of curvature are less than twice the periostracal thickness'. Even within the freshwater cementers, Gregoire (1974) noted that although the periostracum of the unionid *Etheria* is thick over the non-cementing part of the shell, over the attachment scar it is considerably thinned. The two clades of cementing bivalves which do have more substantial periostraca, *Cleidothaerus* and *Myochama* are anomalodesmatans. Morton (1974) suggested that *Cleidothaerus* cements by means of a 'sticky' outer periostracal layer, presumably analogous to the secretions of the arenophilic glands of other pandoroids (Prezant 1981; Morton 1987). If this is correct, the problem of creating close proximity between the bivalve and the substratum is solved by the fluid nature of this outer layer.

The possession of an ultra-thin periostracum by free-living bivalves is considered to be less significant for two reasons. First, in contrast with the other life habits recognized here, all free-living bivalves belong to a single major clade, the pteriomorphs. Although undoubtedly polyphyletic within that clade, virtually all pteriomorphs measured had ultra-thin periostraca and hence constancy in this autecological category can be assumed to result primarily from their phylogenetic legacy. Any putative advantages of possessing such a thin periostracum, for example as suggested by Moore and Trueman (1971) in the reduction of drag in swimming scallops, are likely to be fortuitous secondary benefits shared with non-swimming members of the same family. Second, this life habit represents a 'mixed bag' of occasional swimmers (e.g. some pectinids and limids), recliners (e.g. most pectinids, gryphaeid oysters and placunids) and even free crawlers, in the case of the anomiid *Enigmonia engimatica* (Yonge 1977). There is no immediately obvious reason why a pleurothetic mussel (with its attendant thick periostracum), if it were to exist, should not succeed in a 'free-living' life habit.

Particularly thick periostraca appear to be associated with those bivalves which bore chemically into hard substrates and those which burrow deeply within the sediment. Taylor and Kennedy (1969) first noted that borers generally possess thick periostraca and suggested that it protected them from their own boring secretions. It is now confirmed that each of the seven clades of extant boring bivalves recognized by Vermeij (1987) does indeed possess a thickened periostracum (although I was unable to obtain suitable material of the boring arcoid *Litharca* for the quantitative survey, rather worn valves of *L. saxicava*, from the collections of The Natural History Museum (London), confirmed the presence of a persistent periostracum). It has been demonstrated that members of each of these clades, with the exception of the pholads, use acidic secretions, produced from glands in either the middle or inner mantle fold, to assist, at least partly, with the boring process (Morton 1990). It seems likely, therefore, that the possession of a thick periostracum is preadaptive for the life habit. Suggestions for the adaptive significance of the thick periostracum in deep burrowing clades are rather more problematical. It may offer the shells of those taxa which burrow actively some protection from sediment scour, or, since the interstitial water in many sediments is undersaturated with respect to calcium carbonate (see Davies *et al.* 1989), protection against shell dissolution.

Therefore, it seems likely that the possession of specific types of periostraca has been preadaptive in the evolution of many specialized life habits and that exponents of these habits have evolved from either shallow-burrowing or byssate taxa. The form of the periostracum in these primitive stocks influenced the pathways used by specific clades during the radiation. Clearly, periostracal traits are not the sole factors involved in the acquisition of these specialized habits; cementation requires also the assumption of a pleurothetic habit and the production of a suitable cement (Harper 1992), while boring requires the evolution of acid-secreting glands (Morton 1990) and deep burrowing the development of a powerful foot and extensive mantle fusion to allow siphon formation (Stanley 1968).

The results of this survey also appear to show that surface ornamentation is produced by folding a periostracal sheet of constant thickness, and that the finer the sheet the finer the ornament attainable. There is a simple analogy of attempting origami with cardboard instead of thin paper. Interestingly, Checa (1995) recently published a survey of micro-ornament in ammonoids in which he attributed their formation to folding of the periostracum.

The inability of a periostracal sheet of a given thickness to describe an ornament more intricate than a certain scale can be considered in the light of three limiting models: (1) a space-limited periostracum which is highly flexible and limited only by the need to fit physically into the space between the elements of ornament; (2) an energy-limited periostracum where, if too much energy is stored by bending of the sheet, it will pull free of the shell surface; and (3) a strain-limited periostracum where if the sheet is bent too sharply, it will crack.

It is tempting to attempt to derive a standard equation whereby it is possible to predict the minimum scale of ornamentation that a periostracum of a given thickness could produce (and which conversely could be used perhaps to calculate the periostracal thickness for fossil taxa). Such an

equation would, however, depend upon the constant elasticity of the periostracal sheet, and it seems likely that periostraca composed of heterogenous layers, for example the vacuous central layer of the periostracum of *Mytilus edulis*, or those which appear to possess more fibrous layers, would have a different flexibility from those with a more homogenous structure. Again the periostracum may not be held solely responsible for the evolution of shell ornament. Certainly, the very small scale tubercles on the external surfaces of trigoniids are, as noted previously, the result of individual crystals standing proud. Waller (1972) described how, amongst the pectiniform bivalves (all of which have ultra-thin periostraca), those with outer calcareous shell layers of foliated calcite (e.g. Pectinidae) are able to form shells with sharper radial corrugations and projecting spines and squamae than the generally smoother propeamussids with their outer prismatic shell layers. He attributed this to the smaller size of the microstructural elements which make up foliae rather than prisms, thus enabling the former to take up finer surface ornamentation. This idea is persuasive but is not perhaps the whole story, as many of the pinnids bear intricate hyote spines despite having an outermost prismatic shell layer. That the microstructural unit does not necessarily define the minimum scale of the ornament of bivalves with an outer prismatic shell layer was shown by Carriker *et al.* (1980), who illustrated the external surfaces of prisms in modern oysters which show distinct keels and furrows. This observation has been repeated for the outer surfaces of Jurassic gryphaeid oysters (Todd and Harper, unpublished data). In these cases the delicate keels and intervening furrows must be produced by minute deflections of the ultra-thin periostracal sheet on to which the prism was seeded.

There is a number of advantages that accrue to bivalves able to produce intricate shell ornamentation. Logan (1974) considered a number of functions for the spiny outgrowths of spondylids, which might easily be applied to similar structures in other epifaunal taxa. These include defence (either directly or by promoting camouflaging epibionts), assistance with attachment and stability and protection from fouling. Similarly infaunal bivalves may be shown to gain defensively (Carter 1967) or from stabilization within the sediment (Savazzi 1985). It seems likely, therefore, that the possession of a thick, inflexible periostracum may have been an important constraint in preventing certain bivalve groups from exploiting these morphological benefits. Thomas (1978) regarded the arcoids as having been limited in their evolutionary potential by the relative inflexibility of key elements of their body plan such as shell microstructure, a weak ligamenture and dentition. To this list may be added their thick periostraca and it seems likely that the mussels too have been constrained from great morphological diversity by this trait. No doubt both epifaunal mytiloids and arcoids would benefit in their exposed life habits from the ability to form spines and flanges but they have been unable to produce any more elaborate shell ornament than the coarsest of ribbing (e.g. *Geukensia* and *Septifer*). Such disadvantages may be mitigated, at least in part, by the evolution of periostracal hairs, which may be shown to have some defensive and stabilizing value (Bottjer and Carter 1980; Wright and Francis 1984). Similarly the inability to form intricate micro-ornament may be solved, again partially, by the evolution of prefabricated calcareous bodies which can then be incorporated into the periostracum, as described by Aller (1974) for the anomalodesmatan *Laternula*.

THE FOSSIL RECORD AND THE EVOLUTION OF THE PERIOSTRACUM

If the form of the bivalve periostracum has played a vital rôle in their evolution, it would be interesting to know how it has altered over geological time. It might then be possible to answer questions such as whether certain traits are preadaptive or adaptive to certain habits or morphologies.

If we accept that the bivalves are a monophyletic group then we must presumably accept that the great variety of periostraca observed in modern representatives is a result of evolution, influenced by different selection pressures away from a primitive periostracum. Presumably thickening and thinning may be achieved either by addition or subtraction of periostracal layers or by varying the thickness of individual layers. But what was the nature of the primitive

periostracum? Clark (1976) considered that this was a question that we could never answer but suggested that the ultra-thin periostraca of oysters and scallops are just as derived as the very thickened sheets of mytiloids. Given the apparent distribution of periostracal thickness within the class (Text-fig. 2A), and the characteristics of those bivalves, such as the protobranchs, which are considered to show a number of primitive characteristics (Morton 1996), it seems likely that the primitive periostracum was moderately thick. Direct evidence, however, is difficult to muster because, as noted above, the preservation potential of periostracum is very low. Nevertheless, there is a small number of instances where periostracal preservation has been reported (see Table 6) and

TABLE 6. Instances where periostracum preservation has been recorded. § = Crampton (1990); † = Hudson (1968); * = Kříž (1972).

Taxon	Clade	Thickness (μm)	Age
Pholadidea wiffenae §	anomalodesmatan	> 5	late Cretaceous
Praemytilus strathairdensis †	mytiloid	5–15	mid Jurassic
Cardiola alata *	arcoid	30–60	late Silurian
Cardiola tix *	arcoid	30–60	late Silurian

Dr T. J. Palmer has pointed out to me that Pojeta (1978, pl. 15, fig. 6) figured a specimen of the mytiloid *Modilopsis* cf. *modiolaris* which has a substantial outer layer which could be interpreted as periostracum. It is not surprising that the rare cases where bivalves have been preserved with their periostracum are those that belong to clades whose modern representatives have particularly thick periostraca. Comparison of the figures given in Table 6 with the Recent data set show that each falls within the modern range of their respective clades. As noted by Harper and Skelton (1993a), the value for the Jurassic mytiloid is lower than that recorded for most extant mussels, but we cannot tell if these periostraca were preserved intact. Further cases are required before it would be possible to test whether there has been a post-Jurassic selective thickening of the mussel periostracum (perhaps in response to the radiation of boring gastropod predators; Harper and Skelton 1993b).

Undoubtedly the preservation of fossil periostraca is biased towards those taxa with thicker periostracal sheets, and in any case is an exceptional event. A possible avenue for the study of periostracum evolution may be afforded by the examination of ornamentation. Very few Palaeozoic bivalves bear intricate ornamentation and Vermeij (1987) suggested that the first spiny bivalves appeared in the Carboniferous. Although it might be argued that this early lack of ornamentation may be due to the lack of an appropriate extrinsic cue, most obviously intense predation pressure, which would favour its evolution (see Vermeij 1987; Harper and Skelton 1993b), it might equally be plausible to suggest that it was an intrinsic constraint, i.e. possession of an at least moderately thick periostracum, that prevented it.

CONCLUSIONS AND IMPLICATIONS FOR OTHER GROUPS

Periostracal thickness has been shown to be an extremely variable character amongst members of the Bivalvia but within specific clades the range of variation is much narrower. It is suggested that difference in periostracal thickness has played a vital rôle in the evolution of the various bivalve clades, by determining the pathways open to them. Periostracal thickness has been important in the evolution of specific specialized life habits and of different styles of ornamentation.

A similar study may also prove enlightening in investigating the evolution of other invertebrate groups. As noted in the introduction, the basic shell secretion mechanism used by the Bivalvia is used by all Recent members of shell-bearing molluscan classes, with the exception of the Polyplacophora. The possession of a periostracum and this mechanism can be regarded as primitive

for the phylum, and it seems intuitively obvious that all ancient members of these groups would have had periostraca. In particular, a study of the variation of periostraca in Recent gastropods (which do seem to have a great range of thickness) and any link that this might have with styles of ornamentation and life habit might be particularly rewarding. Additionally, there is scope for consideration of the brachiopods. Members of this phylum also secrete their shells on to an outer organic sheet, also termed the periostracum (see Williams and Mackay 1979). The structure is analogous but not homologous to the molluscan periostracum, and there are key differences in the manner in which the mineralized shell material is applied to the periostracum, most notably that it is secreted directly by the cells in the outer mantle lobe rather than by an extrapallial fluid. However, many aspects, such as the flexibility of the periostracal sheet and its implications for micro-ornament, must be similar to those found in molluscs and, therefore, the effects of variation of the periostracum are worthy of investigation.

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APPENDIX

Average periostracal thicknesses and locality data for each species investigated herein. Where the data have been extracted from the literature, either as values given by other authors or determined from published micrographs, the reference is given.

Taxon	Average periostracal thickness (μm)	Locality
Protobranchs		
Acila divaricata	42	Arabian Coast
Ennucula obliquaa	15	Malabar, N.S.W., Australia
Leda minuta	3	Loch Goil
Malletia obtusa	8	Norway
Nucula nitida	10	Millport, Scotland
Nucula nucleus	3	Millport, Scotland
Nucula sulcata	25	Millport, Scotland
Nucula turgida	10	Unknown
Saturnia sulcata	10	Argentina
Solemya australia	100	Taylor *et al.* (1969)
Solemya borealis	100	Maine, USA
Solemya occidentalis	29	Kenya
Solemya parkinsoni	140	Beedham and Owen (1965)
Solemya velum	10	Rhode Island, USA
Yoldia eightsei	31	Signy Island, Antarctica
Yoldia hyperbola	23	Greenland
Yoldia thracinae	13	North-west Atlantic
Yoldiella sabrina	5	Weddell Sea, Antarctica
Arcoids		
Anadara erthraensis	57	Unknown
Anadara ferrugianea	10	Gulf of Papua
Anadara grandis	8	Panama
Anadara trapeziana	100	Port Jackson, N.S.W., Australia
Arca tortuosa	17	Unknown
Arcopsis solida	10	Naos, Panama
Barbatia rostae	35	Naos, Panama
Barbatia helbergi	8	Kenya
Barbatia obliqua	200	Unknown
Barbatia sp.	10	Panama
Glycymeris flamea	2	Two Fold Bay, N.S.W., Australia
Glycymeris glycymeris	11	North Sea
Glycymeris holosericus	45	Jervis Bay, N.S.W., Australia
Glycymeris maculata	24	Bottjer and Carter (1980)
Limatula hodgsoni	1	Weddell Sea, Antarctica
Limopsis enderbyensis	9	Weddell Sea, Antarctica

Taxon	Average periostracal thickness (μm)	Locality
Limopsis marioensis	5	Weddell Sea, Antarctica
Modiolarca tulipa	14	Millport, Scotland
Scapharca globosus	100	Unknown
Scapharca inaequivalvis	54	Unknown
Mytiloids		
Adipicola pelagica	15	Shetland
Adula californianus	47	Washington (Carter 1990)
Adula falcata	19	New Zealand
Amygdalum beddomei	32	Cape Banks, Sydney, N.S.W., Australia
Aulacomya ater	81	Peru (Carter 1990)
Austromytilus rostratus	75	Two Fold Bay, N.S.W., Australia
Bathymodiolus sp.	110	Hook and Golubic (1988)
Bathymodiolus thermophilus	15	East Pacific (Carter 1990)
Botula cinnamonea	24	Kenya
Botula siliqua	50	Marlborough Sound, New Zealand
Brachidontes granulatus	15	Bottjer and Carter (1980)
Brachidontes niger	6	Lagos, Nigeria
Brachidontes rostratus	35	Victoria, Australia
Brachidontes variabilis	15	Tai Tam, Hong Kong
Choromytilus chorus	400	Chile
Cibiticola lunata	5	Cape Ginger
Crenella decussata	5	Carter (1990)
Crenella discors	10	Unknown
Crenella glandula	11	Massachusetts, USA
Fluviolamatus amarus	14	Woolgoolga, N.S.W., Australia
Geukensia demissa	92	North America
Hormomya mutabilis	15	Cape d'Aguilar, Hong Kong
Ischadium recurvum	15	West Florida (Carter 1990)
Limnoperna sinensis	28	China
Lioberus castaneus	22	Bottjer and Carter (1980)
Lioberus salvadoricus	8	Panama
Lithophaga sp.	45	Telegraph Bay, Hong Kong
Lithophaga aristata	8	Naos, Panama
Lithophaga cumingiana	29	Masirah Island, Oman
Lithophaga erthraensis	27	Red Sea
Lithophaga kuehneti	11	Oman
Lithophaga kuentienti	5	Oman
Lithophaga lima	14	Oman
Lithophaga nasuata	25	Aldabara
Lithophaga nigra	21	Carter (1990)
Lithophaga teres	16	Addu Aldabra
Modiolus indet.	10	Galeta, Panama
Modiola striatula	53	Siput Fedo, Malaysia
Modiolus americanus	7	West Atlantic (Carter 1990)
Modiolus areolatus	13	Two Fold Bay, N.S.W., Australia
Modiolus barbatus	25	Unknown
Modiolus capax	80	Naos, Panama
Modiolus elongatus	60	Moreton Bay, Queensland, Australia
Modiolus metcalfei	30	Wu Kwai Sha, Hong Kong
Modiolus modiolus	50	Firth of Lorn, Scotland
Modiolus pseudotulipus	35	Coco del Mar, Panama
Musculista senhausia	34	Tai Tam Bay, Hong Kong

Taxon	Average periostracal thickness (μm)	Locality
Musculus cumigianus	20	Narrabean Beach, N.S.W., Australia
Musculus laevigatus	428	Hokkaido, Japan
Musculus marmatus	10	Unknown
Musculus nanus	50	Two Fold Bay, N.S.W., Australia
Mytella guayensis	15	Panama (Carter 1990)
Mytilospsis domingensis	4	Grand Cayman
Mytilus californianus	294	La Jolla, California
Mytilus edulis	35	Two Fold Bay, N.S.W., Australia
Parapholas californica	20	Carter (1990)
Perna canaliculus	152	New Zealand
Perna palliopunctatus	75	Bottjer and Carter (1980)
Perna perna	160	Zululand, S. Africa
Perna pictus	43	Algiers
Perna viridis	45	Wu Kwai Sha, Hong Kong
Septifer bilocularis	36	Wu Kwai Sha, Hong Kong
Septifer virgatus	60	Cape d'Aguilar, Hong Kong
Stavelia horrida	90	Keppel Bay, Queensland, Australia
Stavelia torta	75	Unknown
Trichomya hirsutus	100	Unknown
Trisodos semitorta	5	Unknown
Unknown modiolid	37	San Felipe Market, Panama
Xenostrobus securus	61	Port Stephen

Pteriomorphs

Taxon	Average periostracal thickness (μm)	Locality
Adamussium colbeci	< 1	Weddell Sea, Antarctica
Aequipecten gibbosus	< 1	Unknown
Alectryonella cremulifera	< 1	Hong Kong
Alectryonella haliotoidea	< 1	Hoi Sing Wan, Hong Kong
Amussium ballotti	< 1	Broken Bay, N.S.W., Australia
Amussium caudacum	< 1	Zanzibar
Amussium papiraceum	< 1	Caribbean, Panama
Amussium pleuronectes	< 1	Unknown
Anomia archaeus	8	Seychelles
Anomia descripta	< 1	Two Fold Bay, N.S.W., Australia
Anomia ephippium	10	Galway, Eire
Atrina inflata	< 1	Sai Kung Market, Hong Kong
Atrina maura	< 1	Panama
Atrina pectinata	< 1	Cape d'Aguilar, Hong Kong
Atrina vexillum	< 1	Zanzibar
Chlamys asperrinus	< 1	Victoria, Australia
Chlamys opercularis	< 1	Dunstaffnage Bay, Scotland
Chlamys pusio	< 1	Galway Bay, Eire
Chlamys senatoria	< 1	Seychelles
Chlamys varia	< 1	Galway Bay, Eire
Crassostrea angulata	< 1	Courseilles, France
Crassostrea gigas	< 1	Ministry of Agriculture and Fisheries
Crassostrea virginica	< 1	Carriker *et al.* (1980)
Decatopecten plica L.	< 1	Unknown
Dimya corrugata	< 1	Australia
Electroma alacorvi	< 1	Paula Salu, Singapore
Enigmonia aenigmatica	< 1	Singapore
Equichlamys bifrons	< 1	Coffin Bay, South Australia
Foramelina exempla	< 1	Sydney, N.S.W., Australia

Taxon	Average periostracal thickness (μm)	Locality
Hinnites giganteus	< 1	Canadian Shellfisheries
Hyotissa hyotissa	< 1	Addu Atoll, Maldives
Hyotissa latissimus	< 1	Maldives
Hyotissa numissina	< 1	Oman
Hyotissa sinensis	< 1	Hong Kong
Isognomon bicolor	< 1	Unknown
Isognomon dentifer	< 1	Oman
Isognomon ephippium	< 1	Tai Tam Harbour, Hong Kong
Isognomon janus	< 1	Naos, Panama
Isognomon legumen	< 1	Cape d'Aguilar, Hong Kong
Isognomon perna	< 1	Aldabara, Maldives
Isognomon recognitus	< 1	Naos, Panama
Lima colrata	< 1	New Zealand
Lima excavata	< 1	Norway
Lima fragilis	< 1	Hervey Bay, Queensland, Australia
Lima hians	< 1	Millport, Scotland
Lima lima	< 1	Grand Cayman
Lima scabra	< 1	Belize
Lyropecten antillarum	< 1	Grand Cayman
Malleus regula	< 1	Oman
Melina samoensis	< 1	Ellice Island, Pacific
Minnachlamys gloriosa	< 1	Moreton Bay, Queensland, Australia
Monia squama	10	Galway, Eire
Neopycnodonte cochlear	< 1	Atlantic Ocean
Neopycnodonte hyotissa	< 1	Fairfax Island, Queensland, Australia
Ostrea angasi	< 1	Two Fold Bay, N.S.W., Australia
Ostrea conchophila	< 1	Naos, Panama
Ostrea edulis	< 1	Galway Bay, Eire
Ostrea irridesceus	< 1	Naos, Panama
Ostrea virescens	< 1	Manly, N.S.W., Australia
Pecten diegensis	< 1	Clark (1974)
Pecten fumatus	< 1	Long Beach, Sydney, N.S.W., Australia
Pecten jacobeus	< 1	Atlantic Ocean
Pecten maximum	< 1	Millport, Scotland
Pedum spondyloideum	< 1	Shimoni, Kenya
Pinctada margaritacea	< 1	Aldabra Atoll
Pinctada martensii	< 1	Cape d'Aguilar, Hong Kong
Pinctada radiata	< 1	Addu Atoll, Maldives
Pinna bicolor	< 1	Zanzibar
Pinna carnea	< 1	Grand Cayman
Pinna deltoides	< 1	Townsville, Queensland, Australia
Pinna menkei	< 1	Vaucluse Bay
Pinna rudis	< 1	Unknown
Pinna saccata	< 1	New Caledonia
Placunonnia foliata	10	Mediterranean Sea
Plicatula plicata	< 1	Tolo Channel, Hong Kong
Plicatula imbricata	< 1	Phuket, Thailand
Pseudanussium septenradiata	< 1	Millport, Scotland
Pteria brevialata	< 1	Hong Kong
Pteria atlantica	< 1	Ghana
Pteria chinensis	< 1	Maldives
Pteria penguin	< 1	Hoi Sing Wan, Hong Kong
Saccostrea sp.	< 1	Galetos, Panama

Taxon	Average periostracal thickness (μm)	Locality
Saccostrea commercialis	< 1	Lizard Island, Queensland, Australia
Saccostrea cucullata	< 1	Tai Tam Bay, Hong Kong
Scaeochlamys livida	< 1	Unknown
Semipallium tigris	< 1	Mombasa
Spondylus americanus	< 1	Tropical Shellfish Suppliers
Spondylus ducalis	< 1	Tolo Channel, Hong Kong
Spondylus marisrubri	< 1	Oman
Spondylus sp.	< 1	Hong Kong
Stabilima strangei	< 1	Port Jackson, N.S.W., Australia
Streptopinna saccata	< 1	Addu Atoll, Maldives
Striostrea margaritacea	< 1	Sri Lanka
Vulsella vulsella	< 1	Cook Island, N.S.W., Australia
Lucinoids		
Ambuscintilla praemium	2	Two Fold Bay, N.S.W., Australia
Anodontia edentula	10	Kenya
Codakia tigerina	3	Kenya
Corbis fimbriata	5	New Caledonia
Ctena divergans	5	Kenya
Diplodonta codakia	8	Mirs Bay, Hong Kong
Diplodonta diplodonta	10	Ghana
Diplodonta globulosa	5	North Heads, Sydney, N.S.W., Australia
Diplodonta lateralis	5	Kenya
Diplodonta tellinoides	6	Naos, Panama
Galeomma sp.	1	Unknown
Kellia adamsi	5	Unknown
Lasaea australis	3	Two Fold Bay, N.S.W., Australia
Loripes clausus	2	Watanua, Kenya
Loripes lucinalis	3	Isle of Wight, England
Lucina pennsylvanica	5	Grand Cayman
Lucina rugifera	2	Shell Harbour, N.S.W., Australia
Montacutona compacta	5	Morton (1980*a*)
Montacutona olivacea	5	Morton (1980*a*)
Myrtea botanica	10	Malabar, N.S.W., Australia
Myrtea spinifera	1	Unknown
Parathysira resupina	8	Cronulla, N.S.W., Australia
Parvilucina fieldingi	3	Oman
Phacoides borealis	5	Outer Hebrides, Scotland
Unknown erycyinid	6	Unknown
Heteroconchs		
Abra alba	30	Millport, Scotland
Abra milaschewichi	2	Black Sea, Rumania
Acanthocardia echinata	1	Millport, Scotland
Americardia media	2	Unknown
Angulus tenuis	1	Oban, Scotland
Angulus tenuis	2	Millport, Scotland
Anomalocardia squamosa	1	Hoi Sing Wan, Hong Kong
Arctica islandica	70	Millport, Scotland
Asaphis deflorata	5	Addu Atoll, Maldives
Astarte borealis	83	Komandor Island, N. Pacific
Astarte compressa	5	Arctic

Taxon	Average periostracal thickness (μm)	Locality
Astarte elliptica	26	Dunstaffnage Bay, Scotland
Astarte sulcata	29	Millport, Scotland
Astarte willeti	10	Gulf of Alaska
Atactodea glabrata	1	Addu Atoll, Maldives
Atactodea striata	1	Addu, Maldives
Bassina multilamellata	1	Hoi Sing Wan, Hong Kong
Calyptogena magnifica	60	Lutz *et al.* (1994)
Cardita affinis	1	San Felipe Market, Panama
Cardita astartoides	10	Kengelan Islands
Cardita laticosta	2	Naos, Panama
Cardita variegata	2	Tolo Channel, Hong Kong
Cerastoderma edule	2	Dunstaffnage Bay, Scotland
Cerastoderma glaucum	1	Sussex, England
Cerastoderma lamarkii	1	Wells, Norfolk, England
Chama aspersa	1	Aldabra Atoll
Chama buddiana	1	Naos, Panama
Chama fibula	1	Moreton Bay, Queensland, Australia
Chama imbricata	1	Aldabara Atoll
Chama jukesii	1	Great Barrier Reef, Australia
Chama lazarus	1	Philippines
Chama reflexa	1	Cape d'Aguilar, Hong Kong
Chama solida	1	Naos, Panama
Chamalea gallica	20	Millport
Chione mariae	1	Panama
Chione subrugosa	1	Panama
Circumphalus cassina	3	Millport, Scotland
Claudioconcha japonica	1	Tai Tam Bay, Hong Kong
Clausinella fasciata	3	Millport, Scotland
Clementia crassiplica	1	Broome, Western Australia
Clinocardium nutalli	2	Unknown
Caecella chinensis	4	Hong Kong
Coelomactra antiqua	14	Sai Kung Market, Hong Kong
Congeria cochleata	7	North Sea
Corbula crassa	89	Tolo Channel, Hong Kong
Corbula gibba	100	Millport, Scotland
Corbula smithiana	100	Two Fold Bay, N.S.W., Australia
Corbula sp.	50	Panama, Naos
Crassatella florida	2	Florida Keys
Cutellus lacteus	20	Thailand
Cutellus hanleyi	16	Unknown
Cyclocardia australoidea	2	Weddell Sea, Antarctica
Cyclocardia borealis	2	Bottjer and Carter (1980)
Donacilla carnea	17	Turkey
Donax cueatus	8	Thailand
Donax faba	10	Wu Kwai Sha, Hong Kong
Donax obesus	2	Panama
Donax panamensis	2	Naos, Panama
Donax scalpellum	10	Oman
Donax variabilis	3	Florida
Donax vittatus	25	Oban
Dosinia dunkeri	10	San Felipe Market, Panama
Dosinia exoleta	10	Millport, Scotland

Taxon	Average periostracal thickness (μm)	Locality
Ensis directus	60	Narangasett Bay, USA
Ensis ensis	30	Dunstaffnage Bay, Scotland
Ensis siliqua	50	Millport, Scotland
Etheria elliptica	14	West Africa
Eucrassaella kingicola	40	South West Australia
Eucrassatella cummingii	23	Hervey Bay, Queensland, Australia
Eucrassatella cummingii	30	N.S.W., Australia
Fabula nitida	4	Kawaguti and Ikemoto (1962)
Florimetis cognatus	2	San Felipe Market, Panama
Gafrarium divaricatum	28	Cape d'Aguilar, Hong Kong
Gafrarium tumidum	5	Hoi Sing Wan, Hong Kong
Gaimardia finlayi	5	Morton (1979a)
Gaimardia trapeziana	2	Discovery Expedition
Gari fervensis	5	Millport, Scotland
Glauconometta plankta	8	Two Fold Bay, N.S.W., Australia
Glossus humanus	100	Lyn of Lorn, Scotland
Glossus vulgaris	15	Unknown
Iphigena brasilliana	30	Florida, USA
Kellia suborbicularis	10	Friday Harbour, Washington, USA
Laevicardium crassum	70	Plymouth, England
Lutraria angustior	8	Northern Atlantic Ocean
Macoma balthica	5	Wexford, Eire
Macoma grandis	2	Panama
Macoma tenta	5	Trinidad
Macrocallista maculata	20	Bevelander and Nakahara (1967)
Mactra corallina	3	Scotland
Mactra fonescana	10	San Felipe Market, Panama
Mactra laevicardia	8	Cockle Cove, Patagonia
Mactra mera	1	Tolo Channel, Hong Kong
Meretrix costa	6	Unknown
Meropesta nicobarica	10	Oman
Mulinia pallida	1	Bicque, Panama
Nemocardia bechei	10	Seychelles
Neotrigonia bednalli	4	St Francis Island, Southern Australia
Neotrigonia gemma	3	Malabar, Sydney, N.S.W., Australia
Neotrigonia margaritacea	8	Morton (1987b)
Neotrigonia sp.	12	Taylor et al. (1969)
Notocallista diemensis	3	Long Bay, N.S.W., Australia
Notospisula parva	1	Gosford, N.S.W., Australia
Nutallia ezonis	10	Hokkaido, Japan
Orbiculana orbiculata	33	Penang, Malaysia
Periglypta multicostata	2	Panama
Periglypta retisulcata	1	Yeppoon, Queensland, Australia
Petricola lucasana	2	Naos, Panama
Pharaonella perna	20	Funzi, Kenya
Pharella javanica	15	Unknown
Pharella acutidens	4	Tsu Sha Tsui Market, Hong Kong
Pharella japonica	18	Sungei, Malaysia
Pharella jouanettia	10	Sungei, Malaysia
Phaxas cutellus	5	Kenya
Pitar tortuosa	1	Panama
Placamen molimen	2	Long Bay, N.S.W., Australia
Plagiocardia setosa	1	Hervey Beach, Queensland, Australia

Taxon	Average periostracal thickness (μm)	Locality
Plebidonax deltoidea	5	Woolgoolga, N.S.W., Australia
Polymesoda inflata	23	San Francisco, Panama
Prototharca grata	1	Panama
Prototharca megintyi	1	Panama
Psammotellina semmelinki	15	Thailand
Psamorbid sp.	12	Clyde River, N.S.W., Australia
Pseudopythina subsinuata	14	Hong Kong
Quadrans gargadia	10	Aldabra
Quidnipagus palatau	3	Kenya
Quidnipagus palatum	2	Maldives
Raeta plicatella	2	Sanibal Island
Sanguinolatia donacioides	8	Lake Irrawarra, N.S.W., Australia
Schizothaerus sp.	70	British Columbia
Scintilla sp.	2	Tolo Channel, Hong Kong
Scintilla striata	1	Oman
Scrobicularia plana	2	Millport, Scotland
Sinovacula sp.	6	China
Solecurtus chamasolen	5	Unknown
Solecurtus divaricatus	10	Carter (1990)
Solen cylindraceus	8	Port Elizabeth
Solen marginatus	10	Unknown
Solen regularis	100	Thailand
Solen sicarius	62	Tofino, British Columbia
Solen sp.	10	Tai Tam, Hong Kong
Solen vitreus	4	Unknown
Soletellina vitatacea	4	Kokan, India
Sphenia binghami	5	Oban, Scotland
Spisula calcar	5	Unknown
Spisula elliptica	30	Millport, Scotland
Spisula solida	10	Millport, Scotland
Spisula subtruncata	2	Millport, Scotland
Strigilla eutronia	5	Ingham, Queensland, Australia
Tagelus dombei	63	Panama
Tagelus politus	16	San Felipe Market, Panama
Tagelus sp.	50	San Felipe Market, Panama
Tapes philippinarum	5	Hoi Sing Wan, Hong Kong
Tellina deltoidalis	5	Two Fold Bay, N.S.W., Australia
Tellina donacina	1	Unknown
Tellina donacina	2	Atlantic Ocean
Tellina fabula	2	Atlantic Ocean
Tellina tenuis	4	Scotland
Theora fragilis	10	Queensland, Australia
Tivela compressa	10	Kenya
Trachycardium maculosum	1	Northern Oman
Trachycardium sp.	1	Addu Atoll, Maldives
Transenella puella	2	Naos, Panama
Trapezium sublaevigatum	110	Morton (1979b)
Tridacna crocea	2	Lizard Island, Queensland, Australia
Tridacna maxima	1	Cook Islands
Venericardia amabilis	2	Long Bay, N.S.W., Australia
Venerupis pullastra	5	Loch Torridon, Scotland
Venerupis senegalensis	25	Millport, Scotland
Venus ovata	1	Addu Atoll, Maldives

Taxon	Average periostracal thickness (μm)	Locality
Vepricardium asiaticum	1	Unknown
Vepricardium sinensis	1	Unknown
Anomalodesmatans		
Aspidopholas objecta	23	Lau Fau Shan, Hong Kong
Cleidothaerus albidus	7	N.S.W., Australia
Cleidothaerus maorianus	10	Morton (1974)
Cochlodesma praetenua	3	Northumberland, England
Coralliophaga coralliophaga	15	Morton (1980b)
Corbula porcina	3	Montevideo, Uruguay
Cuspidaria latesulcata	10	Cape Banks, Sydney, N.S.W., Australia
Cuspidaria rostratus	10	Norway
Cuspidaria tenella	5	South Orkney
Cyrtodaria siliqua	33	N. Europe
Ectorisma granulata	2	Malabar, Sydney, N.S.W., Australia
Fulvia mutica	1	Tai Tam Bay, Hong Kong
Gastrochaena cuneiformis	8	Kenya
Gastrochaena dubia	18	Eire
Gastrochaena hians	10	Carter (1978)
Gastrochaena mytiloidea	10	Kenya
Gastrochaena ovata	8	Carter (1978)
Hiatella arctica	40	Millport, Scotland
Hiatella australis	2	Two Fold Bay, N.S.W., Australia
Hiatella orientalis	11	Hoi Sing Wan, Hong Kong
Hiatella striata	8	Fowey, Cornwall, England
Jouannetia cumingi	2	Phuket, Thailand
Laternula elliptica	10	Unknown
Laternula flexuosa	3	Aller (1974)
Laternula gracilis	5	Western Point, Victoria, Australia
Laternula moratina	2	Lake Macquarie, N.S.W., Australia
Lyonsia norwegica	80	Northumberland, England
Lyonsia californica	5	San Juan Island
Lyonsia hyalina	3	Naragansett Bay, USA
Martesia striata	10	Cape d'Aguilar, Hong Kong
Mya japonica	15	China
Mya truncata	20	Dunstaffnage Bay, Scotland
Myadora complexa	15	Sydney, N.S.W., Australia
Myochama anomioides	14	N.S.W., Australia
Myochama strangei	60	Port Jackson, N.S.W., Australia
Offadesma angasi	3	New Zealand
Parapholas quadrizanatta	8	Oman
Pholas sp.	10	Naos, Panama
Pholas dactylus	5	Margate, Kent, England
Pholas parva	10	Devon, England
Saxicava rugosa	20	Brighton, England
Spengleria rostrata	15	Carter (1978)
Sphenia fragilis	10	Naos, Panama
Thracia beningi	5	Cook Inlet, Alaska
Xylophaga dorsalia	10	Unknown